

SOME PHYSIOLOGICAL VARIATIONS IN THE
BLACK-CAPPED CHICKADEE

BY EUGENE P. ODUM

IN addition to field observations already reported (Odum, 1941-42), I carried out, in 1939-40, a series of laboratory experiments on Black-capped Chickadees (*Penthestes atricapillus*) at the Huyck Preserve, Rensselaerville, New York.* Birds were "borrowed" from their natural environment for short periods of laboratory study, and returned uninjured to the field. Since the purpose was to measure the normal wild condition as nearly as possible, birds were kept captive no longer than necessary, never longer than overnight. All birds were banded with colored and numbered bands.

The Black-capped Chickadee provides an especially favorable subject for combination field and laboratory study, since it is easily trapped, is present throughout the year, and since short laboratory confinement seems not to affect its normal behavior out-of-doors or its lack of fear towards man. The measurements made so far only scratch the surface of possible physiological work with this species. The following variables were studied: wing and tail lengths, weight, body temperature, heart rate, breathing rate, and muscle tremors. The latter three variables were measured simultaneously with a special apparatus, the cardio-vibrometer, which has been described elsewhere (Odum and Kendeigh, 1940; Odum, 1941). Simple statistical analysis was made when data seemed to warrant it. Since many samples were small, special formulas for small samples were employed in determining standard errors (see Arkin and Colton, 1939).

DISTINGUISHING OF SEXES

Although colored alike, the sexes in the living Black-capped Chickadee can be easily distinguished during the nesting season by behavior and by the presence of a "brood patch" in the female. At other seasons there is apparently no consistent difference in plumage or behavior, though males appear to be slightly larger, as earlier workers have recorded. The maximum wing lengths (measured with the primaries flattened against the ruler) of 36 Black-capped Chickadees measured in this study ranged from 61 to 69 mm. The sex of 22 was determined by breeding behavior. Of these, 13 were males, and their wings measured consistently more than 64 mm.; 9 were females, and their wings measured consistently less than 65 mm. Consequently, careful wing measurement was an aid in sexing: in the 14 birds whose sex had not been determined by behavior, wing measurements of 66 mm. or more were taken as indicating males; those of 63 mm. or less, females; the sex of

* I am indebted to the officers of the Edmund Niles Huyck Preserve for the opportunity to conduct the experiments, and to S. Charles Kendeigh for critical reading of the manuscript.

birds with wing measurements between 66 and 63 mm. remained undetermined. Tail length varied from 60 to 65 mm., but because of the large overlap in measurements and variation in length due to wear, tail measurements were not an aid in sexing.

BODY WEIGHT

Weight records are summarized according to sex and season in Table 1. Average figures for the Black-capped Chickadee at Gates

TABLE 1
BLACK-CAPPED CHICKADEE WEIGHTS IN GRAMS

		Jan/Feb		Mar/Apr		June		Total		Standard Deviation
		No.	Av.	No.	Av.	No.	Av.	No.	Av.	
Rensselaerville, N. Y.	Male	21	12.4	7	12.7	7	11.4	35	12.2	± 0.68
	Female	8	11.9	5	11.6	5	10.8	18	11.5	± 0.70
	Both sexes	29	12.2	12	12.2	12	11.2	53	12.0	± 0.75
	Sex difference		0.5		1.1		0.6		0.7	± 0.20
Gates Mills, Ohio	Both sexes	36	11.5	42	11.1	10	10.4	88	11.2	± 0.95
	Locality difference		0.7		1.1		0.7		0.8	± 0.15

Mills, Ohio (Baldwin and Kendeigh, 1938), are included for comparison. In order to minimize daily fluctuations, all Rensselaerville weights were taken in the late afternoon, at or near the theoretical maximum in the daily rhythm of weight. Three things of general interest seem to be indicated by these data:

1. Males averaged heavier than females at all seasons investigated (a fact also reported by Baldwin and Kendeigh, 1938). The average difference (0.7 gms.) is statistically significant, since it is more than three times as large as the standard error (0.2 gms.). However, because of the considerable overlap and general variability, weight in this species is not a reliable means of distinguishing sex.

2. Rensselaerville chickadees weighed more than Gates Mills birds. The difference (0.8 ± 0.15 gms.) is easily significant provided we assume that the sex factor and daily rhythm factor are eliminated in the averages; and the difference is to be expected since Rensselaerville has the more northern climate. There appears to be a gradual southward decrease in size as indicated by wing measurements in the Black-capped as well as in the Carolina Chickadee, *Penthestes carolinensis* (see Todd and Sutton, 1936), and there is presumably also a north-south weight gradient, although this has not yet been demonstrated.

3. No difference was found between average winter and average spring weights. January and April records on the same individuals also failed to show any significant difference. But the difference between winter and June weights is significant (1.0 ± 0.19 gms.). Since most

June weights represent birds feeding young it is not known whether the decrease is correlated only with season or is perhaps partly the result of strenuous feeding activities. Seasonal variation in weight is well known, most passerines being heavier in winter than in summer (Nice, 1938; Baldwin and Kendeigh, 1938). In the generalized curve (based on a number of species) given by Baldwin and Kendeigh (1938), weight decreases 7 per cent from January to April and 11 per cent from January to June. Zedlitz (1926), however, has reported that certain European Paridae (*Parus* [*Penthestes*] *atricapillus borealis*, and *P. palustris*) as well as the Magpie (*Pica pica*) are exceptions to this general rule. The White-breasted Nuthatch (Baldwin and Kendeigh, 1938) and Tufted Titmouse (Nice, 1938) seem to show comparatively little seasonal variation in weight. From incomplete data on American chickadees it seems that the seasonal weight rhythm may not be so pronounced as in many other passerines, but since there is a complexity of factors affecting weight, far more data are needed before significant conclusions can be drawn. It should be emphasized that a few weight records from scattered localities are of no value in this connection; large series of weights from local populations are needed.

HEART AND BREATHING RATES

Methods. Because of the great variability of the heart and breathing rates in small birds it is necessary to determine some sort of stabilized rate—a standard or “basal” rate—if useful comparisons are to be made. The basal heart and breathing rates are defined as the average rates when the bird is in a post-absorptive (though not starved) condition, in darkness, away from human presence, and at a controlled (or specified) temperature. The same apparatus and general procedures as described in an earlier publication (Odum, 1941) were used to determine basal rates for the study birds. The individual to be tested was captured in the late afternoon, weighed and measured, kept in the dark for two to three hours, then placed on the sensitive perch within the temperature control chamber. By a simple technique previously described (Odum, 1941), it was easy to get the birds to remain voluntarily on the perch indefinitely, in darkness, and entirely free from outside disturbances. Figure 1 is a flashlight photograph of part of the experimental apparatus, showing a Chickadee resting on the perch crystal in the temperature chamber. The bird is sleeping in the typical pose assumed at lower air temperatures, that is, with head turned back, bill buried in scapular feathers, and feathers fluffed out (the same pose as that observed out-of-doors). The recording apparatus and earphones (in order to keep informed of the bird's general behavior) were in another room. After allowing half an hour or more for the bird to become adjusted to the conditions, records were made at about 15-minute intervals for the next several hours. Thus, all records were made between 8 P.M. and 12 P.M.,

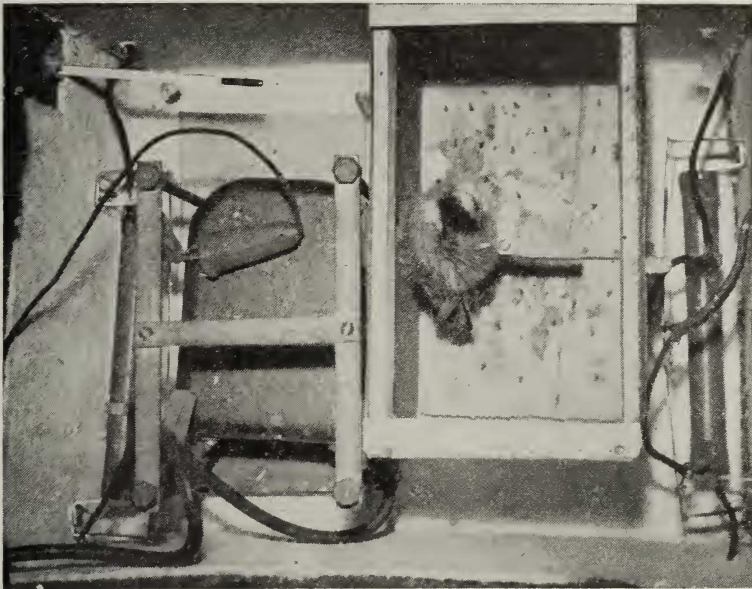


Figure 1. A flashlight photograph of a Black-capped Chickadee sleeping on the perch attached to the piezo-electric crystal (left) within the temperature chamber. The bird has its head turned back, bill buried in scapulars, and feathers greatly fluffed out.

three to seven hours after the last feeding and during the normal roosting time, the period that has previously been found most satisfactory for basal-rate determination. Birds were tested at three temperatures— $90 \pm 1.5^{\circ}\text{F}$. (32.2°C .), $70 \pm 2^{\circ}\text{F}$. (21.1°C .), and $43 \pm 2^{\circ}\text{F}$. (7.5°C .)—each individual usually being tested at two temperatures successively; 90° was thought to be approximately thermal neutral (temperature at which to expect the lowest rate of metabolism); 43° was selected as the lowest conveniently obtainable temperature; 70° is an intermediate point and the usual value of “room temperature.” Unfortunately, the low temperature could not be duplicated during the summer.

In analyzing the graphic records and computing averages, I used the standardized procedure previously described (Odum, 1941). Since breathing rate is relatively slower than heart rate, the number of readings for breathing rate were fewer than those for heart rate, but the averages cover the same period of time. Thirty-four determinations of basal heart and breathing rates, taken from 14 individuals (of which four were measured twice), are given in Table 2. Whereas statistically, this is a small number of records, it is so far the largest series for adults of any wild species to be obtained under comparable controlled conditions.

Sex differences. Since most of the birds studied were males, no conclusion can be drawn regarding the sex factor in heart and breathing rates. Differences, if any, are probably small. Consequently, the sex factor is ignored in most of the following discussion.

Variability. It is interesting to analyze variability since it is a notable characteristic of the heart and breathing rates in small birds. In Figure 2, the variations (during a period of 36 seconds) in the heart rate of a typical individual under the controlled conditions described above are given in detail; readings taken during and between each

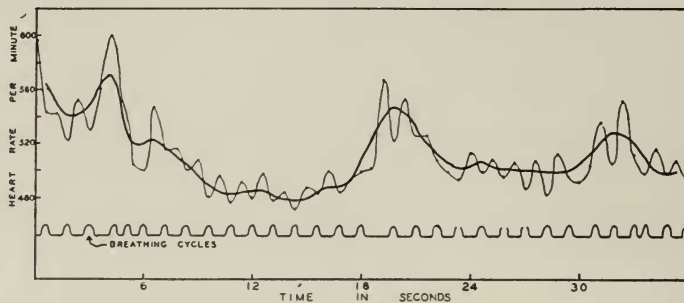


Figure 2. Inherent variations in the heart rate of a typical Black-capped Chickadee (male, June 21). Variations correlated with breathing are superimposed on large oscillatory variations (smoothed curve).

breathing cycle are plotted together with a smoothed curve (representing three "oscillatory" variations), to show the two types of inherent variation in heart rate characteristic of the study birds: 1. Variation which is correlated with the inflation and deflation cycle of the lungs, the heart rate usually decreasing slightly at the peak of the inflation part of the cycle and increasing between cycles. (In mammals, on the contrary, heart rate usually increases during inflation and slows down during deflation—Anrep, Pascual, and Rössler, 1936.) 2. "Oscillatory" fluctuations (Odum, 1941), a more pronounced, slower, and rhythmic (though not usually regular) type of variation. Oscillatory fluctuations may sometimes be related to pauses in breathing (removal of the inhibitory influence of lung inflation mentioned above), or to the action of periodic muscle tremors,¹ but frequently there is no apparent cause (though they are presumably correlated in some way with vagus periodicity). The degree of oscillatory fluctuation varies considerably with individuals; often it can be detected by ear. Inherent

¹ Tremors are defined as coordinated, semi-rhythmic partial muscle contractions or changes in muscle tone which, when pronounced, produce visible shivering. See Odum, 1942:618 or 1941:312.

TABLE 2
BASAL HEART AND BREATHING RATES OF BLACK-CAPPED CHICKADEES

Individual	Sex	Date	Temperature 90±1.5°F.						Temperature 43±2°F.						Temperature 70±2°F.					
			Heart Rate		Breathing Rate		N	sD	Heart Rate		Breathing Rate		N	sD	Heart Rate		Breathing Rate		N	sD
			N	M	N	M			N	M	N	M			N	M	N	M		
A-R	♂?	Jan. 19	33	518	13.6	8	108.0	12.2	11	614	28.3	3	73.0	49	546	50.2	11	76.4	3.6	
A-RY	♂	Jan. 22	29	411	20.9	8	80.4	5.1	27	550	19.8	7	69.8	30	548	25.3	11	51.5	3.4	
A-BY	♂?	Jan. 27	27	538	25.7	8	105.0	6.9	20	582	27.9	6	62.3	25	539	31.2	4	56.0	...	
A-Y	♂?	Feb. 8	45	346	18.2	11	81.3	5.6	27	582	27.9	6	62.3	14	555	23.7	6	64.7	2.6	
A-RG	♂	Feb. 13	35	444	17.1	9	80.0	7.7	20	582	27.9	6	62.3	15	554	31.3	5	50.6	5.8	
A-BI	♀	Feb. 16	33	376	31.9	11	81.3	5.6	20	600	39.2	6	63.7	49	546	50.2	11	76.4	3.6	
A-YR	♂	Mar. 2	58	445	12.9	13	107.7	15.6	25	618	38.6	5	61.6	3.7	548	...	2	58	...	
A-BG	?	Mar. 7	39	458	13.1	7	99.4	10.5	20	600	39.2	6	63.7	4.0	
A-RG	♂	Mar. 15	42	487	18.5	9	86.4	7.4	21	582	31.9	8	64.1	3.7	
A-RG	♂	Apr. 8	23	480	19.5	8	92.2	5.4	19	624	25.5	6	69.2	3.1	
A-BI	♀	Apr. 9	30	368	20.0	8	76.6	2.0	17	627	45.4	7	73.3	6.8	
A-RY	♂	Apr. 11	25	418	21.3	9	77.3	6.1	17	538	28.3	8	67.7	3.3	
A-YR	♂	Apr. 12	21	466	21.6	9	108.3	6.9	17	655	41.0	6	70.2	4.9	
A-YB	♀	Apr. 18	21	466	21.6	9	108.3	6.9	20	639	43.8	7	72.6	5.8	
A-BR	♀	Apr. 24	30	547	25.4	9	88.4	6.6	15	674	36.7	5	56.5	2.0	
B-J	♂	Jun. 11	14	524	17.3	5	65.4	1.7	15	674	36.7	5	56.5	2.0	
B-2	♂	Jun. 20	14	524	17.3	5	65.4	1.7	15	674	36.7	5	56.5	2.0	
R-GR	♂	Jun. 21	15	536	36.4	4	51.0	...	15	674	36.7	5	56.5	2.0	

N = number readings. M = mean sD = Standard deviation.

variations are of interest for at least two reasons: first, they indicate that the heart rate is rarely uniform, and second, a series of readings should be taken in order to avoid any confusion of inherent variations with variations resulting from external factors.

TABLE 3
VARIATION IN HEART AND BREATHING RATE IN BLACK-CAPPED CHICKADEES

	Number of Individuals	Average Coefficient of Variation
A. Intra-individual Variation		
Heart rate: at 90°F.	13	4.53
at 43°F.	12	5.53
Breathing rate: at 90°F.	13	8.50
at 43°F.	11	5.91
B. Inter-individual Variation		
Heart rate: at 90°F.	13	12.50
at 43°F.	12	6.36
Breathing rate: at 90°F.	13	13.10
at 43°F.	11	7.60

In Table 3 the variation in the regular sample readings is indicated by means of coefficients of variation, which simply give a picture of the variation around the mean values. Winter and spring records are combined in order to bring out the effects of temperature and individual variation. Several points of interest are indicated as follows: 1. Heart rate varied somewhat more within the individual at 43° than at 90°, apparently because of the action of periodic tremors. At 90° no tremors were recorded, but at 43° short tremor periods often occurred, accompanied by heart rate fluctuations. The relation of tremors to heart rate and temperature regulation has been discussed elsewhere (Odum, 1941; 1942). 2. Variation in heart rate between different individuals was greater at 90°, a possible indication that 90° is not a good thermal neutral point. 3. Breathing rate, both intra- and inter-individually, was more variable at 90° than at 43°, probably because of the function of the breathing rate in heat loss as explained below. 4. Breathing rate seemed to be slightly more variable generally than heart rate, especially at high temperatures. 5. Basal rates for both heart and breathing were more constant within the individual than between individuals, indicating that both may be considered individual characteristics, as in man. Accordingly, in testing the effect of various factors it is better to use the same individuals if possible. If different individuals are used a larger series is desirable.

Effect of temperature on heart and breathing rates. Average basal rates for all individuals which were tested at the three temperatures during winter and spring are plotted in Figure 3. The principal points shown by these data seem to be: 1. As would be expected, heart

rate increased with a drop in air temperature. The increase seems to be less between 70° and 43° than between 90° and 70°. In winter the average increase in heart rate between 90° and 43° was about 10 per cent, indicating a high tolerance of low temperatures. As can be seen from Table 2, every individual showed a distinct increase in heart rate when changed from a high to a low temperature, although the degree of response varied. 2. It was surprising at first to find that the breathing rate was higher at 90° than at 70° or 43° (a seemingly opposite

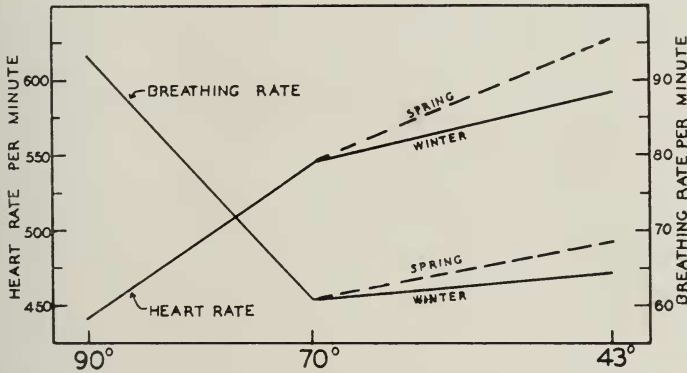


Figure 3. Average standard heart and breathing rates of Black-capped Chickadees at three air temperatures (°F.) during winter and spring. The lines connecting the averages do not necessarily follow the trends (actually unknown) between temperatures. Records at 70°F. are scanty and therefore their averages are not strictly reliable.

response from heart rate). All individuals showed this reaction (Table 2). The explanation is apparently not hard to find, however. Since the lungs and air sacs are one of the principal means of heat loss in birds, the breathing rate is an important part of the heat loss mechanism. Kendeigh (1939) has shown that an abrupt increase in water loss occurs at about 100°F. in both adult and nestling House Wrens; an abrupt increase in breathing rate also occurs in that species at the same temperature (Odum, 1941). In the English Sparrow, however, this critical point is lower—about 85° (Kendeigh, 1934:322). In Black-capped Chickadees the pronounced increase in breathing rate (presumably correlated with increase in water loss) apparently begins somewhere between 70° and 90°; 90° is, then, above the critical point. This explains both the high rate and great variability of breathing at this temperature (Table 3); some readings ran as high as 140 per minute, though at the same time the heart rate was low.

As to the internal mechanism, acceleration of breathing at high temperatures might be reflexive (occurring before a rise in body temperature, as in the dog) or central (that is, due to direct stimulation by

blood temperature rise, of hypothalamic temperature regulation centers). Actual measurement of body temperature of the study birds would have produced many unwanted disturbances, but judging from previous experiments and the low level of heart rate recorded at those temperatures, it would seem unlikely that air temperatures as low as 80° or 90°F. would in this species produce a rise in body temperature. Perhaps, therefore, acceleration of breathing at high temperatures in the Black-capped Chickadee begins reflexively, and this mechanism is augmented by the central "panting" mechanism whenever the body temperature rises. The acceleration of breathing which occurs at low temperatures, on the other hand, can probably be ascribed to increased metabolism and the well-known carbon dioxide mechanism.

The difference in behavior of birds at different temperatures was also striking. At both 43° and 70° (in summer as well as in winter) birds invariably assumed the pose shown in Figure 1, but at 90° the birds did not fluff out their feathers or turn their heads back (the means usually employed to decrease heat loss). Individuals were also more restless at 90°, moving slightly every minute or so, indicating that they were not so comfortable as at the lower temperatures.

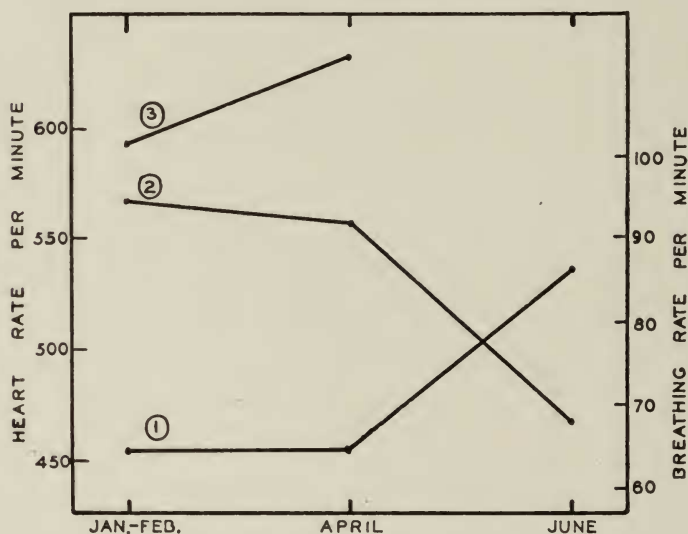


Figure 4. Basal heart and breathing rates at three seasons. (1) Heart rate at 90°F. (2) Breathing rate at 90°F. (3) Heart rate at 43°F.

Effect of season. Seasonal variations in heart and breathing rate are shown in Figures 3 and 4 and Table 2. Because of the small amount of data, only limited comparisons can be made. The basal heart rate at

90° was higher in June than in winter or spring. The average increase was 89 ± 25.1 beats per minute. The difference was also significant when males only were compared. Higher heart rate in summer as compared with the rate in winter at the same temperature is probably correlated with increased metabolism, since basal heart rate is often a good index to metabolism. Kendeigh (1934) found that in English Sparrows the rate of metabolism (as indicated by percentage weight loss) was greater in summer than in winter.

The breathing rate at 90°, on the other hand, was lower in June than in spring or winter (Figure 4). This is undoubtedly related to more rapid heat loss in summer, which may result, at least in part, from less dense plumage and lower weight (Kendeigh, 1934:335). In other words, the critical point previously mentioned (temperature at which breathing shows an abrupt increase) shifts upward in summer, and 90° air temperature no longer results in a high rate of breathing.

Examination of Figure 3 suggests that heart rate may begin to increase in the spring, especially at 43°, since readings for April were usually higher than winter averages. As already pointed out, differences are perhaps more likely to be significant if readings from the same individual are compared. Accordingly, four individuals that had been measured in winter were again tested in April under the same conditions, and the probable significance of the differences was calculated. In April, basal heart rate was significantly higher in all four individuals at 43°, but in only two at 90°. Furthermore, when all data were pooled (irrespective of individual) in order to obtain a large number of readings, the average spring increase at 90° was 16 ± 10.4 (probably not significant), whereas the increase at 43° was 52 ± 11.7 (probably significant). Thus the heart-rate/temperature curve is flatter in winter than in spring (Figure 3).

Discussion. The following generalizations seem to be justified: At intermediate air temperatures, though not at high temperatures, heart rate and breathing rate probably vary directly with each other, and inversely with the temperature. As far as present information goes, basal heart rate may be considered an index to heat production; breathing rate is also related to heat production, but at temperatures above thermal neutral it becomes a rough index to heat loss in birds (as well as in certain mammals). Consequently, the measurement of these vital rates and determination of critical points may reveal much about the bird's response to environmental conditions and its limits of tolerance. The differences between species in these respects may help to explain differences in behavior and distribution. For example, the critical temperature at which breathing shows an abrupt increase is about 100°F. in House Wrens but is appreciably lower in English Sparrows and in Chickadees in winter. Seasonal differences are also striking. In Chickadees the critical point just mentioned seems to shift upward in summer, downward in winter. Likewise, heart rate levels change with the season.

being higher in summer (when the heart rate is presumably correlated with a higher rate of metabolism) and lower in winter. As previously reported (Odum, 1941-42), survival time without food is much higher in winter than in summer. In winter, decrease in heart rate, in metabolism, and in heat loss enable the Chickadee to resist low temperatures. That is, food and shelter are by no means the only considerations in survival. Kendeigh, for example, found that the House Wren, even when food and shelter were amply provided in large cages (where the birds lived successfully through the summer), was unable to survive

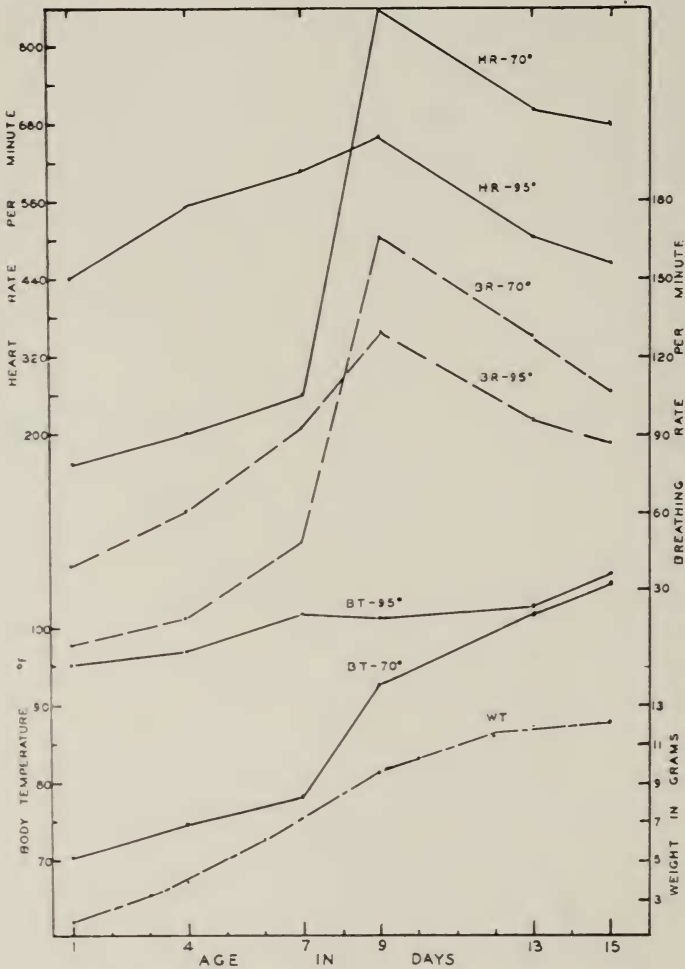


Figure 5. Heart rate (HR), breathing rate (BR), body temperature (BT), and weight (WT) of six ages of nestling Black-capped Chickadees at two air temperatures (95°F. and 70°F.).

northern Ohio winter conditions, presumably because they were unable to make the proper physiological adjustments to temperature. It should be remembered, of course, that the basal rates studied in this paper are but outward manifestations (or net results) of complex internal responses. Seasonal changes, for example, are probably ultimately related to endocrine changes.

DEVELOPMENT OF NESTLINGS

Data on heart rate, breathing rate, body temperature, each at two air temperatures (95°F. and 70°F.), together with the body weight of six ages of nestling Black-capped Chickadees are plotted in Figure 5 for easy comparison. Physiological development of the nestling Chickadee seems not to differ in any important respect from that of the House Wren (Kendeigh, 1938; Odum, 1941) even though the adults may differ. Consequently, only a few points need be mentioned here: 1. As in other altricial species, the Chickadee changes from a cold-blooded to a warm-blooded organism during its nest life. The transition is gradual, but changes are more rapid during the middle third of the 16- to 18-day nest life. Between seven and nine days, the two curves for body temperature (at 70°F. and 95°F.) approach each other (Figure 5, and the two curves for heart rate, as well as those for breathing rate, cross, strikingly illustrating the reversal in the response to temperature. 2. Nestlings (unlike adults in winter) have heart rate and breathing rate closely correlated at the two temperatures used in this study; 95° is for nestlings, therefore, probably below rather than above the critical point in the functioning of the heat loss mechanism. 3. The range of basal heart and breathing rates in nestlings is relatively great when different ages and temperatures are considered, illustrating the great sensitivity of nestlings to small changes in air temperature. 4. The highest heart and breathing rates were recorded at about nine days; muscle tremors were also most intense at this age. As described elsewhere (Odum, 1942), the heat production mechanism seems to develop more rapidly than the ability to control heat loss. At nine days, the feather covering of the nestlings is still poor; consequently, heat loss is poorly controlled, and this probably accounts for the high heart and breathing rates.

SUMMARY

Wing and tail lengths, body weight, body temperature, heart rate, breathing rate, and muscle tremors (the latter three variables being measured with the cardio-vibrometer) of wild Black-capped Chickadees were studied.

Wings ("maximum measurement") varied from 61 to 69 mm., with wings of males as a rule longer; hence wing measurements were an aid in sex distinction. Tail measurements varied from 60 to 65 mm., and were not an aid in sexing.

Males averaged 0.7 ± 0.2 gms. heavier than females. Rensselaerville (New York) birds averaged 0.8 ± 0.15 gms. heavier than Gates Mills (Ohio) birds, when records from the same months were compared. The study birds weighed less in June than in winter, but weight differences between winter and spring were not significant.

There are two types of inherent, more or less rhythmic, variation in heart rate, one correlated with breathing, the other probably of variable cause.

Basal heart and breathing rates were measured at three temperatures, 43° , 70° , and 90° F. With rising temperature heart rate decreased, but at 90° breathing rate increased; this acceleration (probably reflexive) is undoubtedly related to the special role of breathing rate in the control of heat loss, 90° being above the critical temperature, especially for Black-capped Chickadees in winter.

Heart rate probably may be considered a rough index to heat production, and breathing rate a rough indicator of heat loss.

Heart rate was consistently and significantly higher in summer, and usually higher in spring, than in winter. Breathing rate, on the other hand, at 90° was lower in summer than in winter. These changes indicate an important seasonal adjustment of basic physiological rates (including the rate of metabolism), and are undoubtedly significant in the species' successful adaptation to changing seasonal conditions.

Physiological development of the nestlings was similar to that of the House Wren. Weight increase followed a sigmoid curve. Temperature regulation was established gradually, the most rapid changes taking place during the middle third of nest life. A peak in both heart rate and breathing rate was reached at about nine days of age, after which both decreased as the control over heat loss became more effective.

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